NOTES ON LAURACEAE OF TROPICAL AMERICA
I. THE GENERIC STATUS OF NECTANDRA, OCOTEA AND PLEUROTHYRIUM

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Recent collections from the tropics, particularly from South America, have made available materials that in the course of study contributed much towards clarification of our concept of the genera of Lauraceae. It seems appropriate at this point to discuss some of the problems encountered in one of the most controversial areas of the family. Ocotea Aublet and Nectandra Rolander ex Rottboell, wide-spread genera of the tropics of the western hemisphere, represent approximately half of the known species of this region; Pleurothyrium Nees ex Lindley (1836, p. 442)* is a small genus of about twenty species, occurring in northern South America, predominantly in Peru.

A study of the available types in conjunction with pertinent literature shows that taxonomists in general have had a more or less clear concept of Nectandra and Ocotea. Pleurothyrium, however, has been a problem. Careful consideration of the material available, involving a re-evaluation of the literature concerning these genera, leads me to the following conclusion: to date, there is valid reason for maintaining the full generic status of Nectandra and Pleurothyrium apart from Ocotea. It is the comparatively little-known Pleurothyrium that I wish to discuss here. Recent studies of the genus have shed light on staminal structures which, though obviously seen and understood by early students of the family, have not always been clearly described. Until the last quarter century, no adequate illustrations were published.

In general, monographers and authors of floras, following the original description of Nees (1836, pp. 23, 24, 349-351), have accepted Nees' decision in placing Pleurothyrium in Tribe VIII. Dicypellia. The members of the genus are mentioned as trees or shrubs, with sparse, alternate, evergreen, coriaceous,

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* Pleurothyrium, from the Greek words meaning "side" and "little openings" because of the small, lateral valves of the anthers observed particularly in stamens of the first two series.

penninerved leaves, often ferruginous beneath. The inflorescences have been variously described as axillary or terminal, paniculate or thyrsoid, with deciduous bracts; the flowers hermaphrodite, with a 6-parted perianth, coriaceous or fleshy, the lobes (deciduous in fruit) more or less spreading, oblong, the tube obconic; the fruit a berry, immersed, at least in the young state, in the suburceolate tube of the perianth, with spreading-crenate margin. *

Nees has described the perianth of the genus as having 6 "persistent, glandulose lobules" alternating with the lobes of the perianth; 9 perfect stamens, similar structurally, the anthers subcubical, 4-loculed, all of the locules lateral, parallel, ovate, some retrorse, others introrse, the filaments short, the staminodia short, tooth-like, biglandular, the glands originating at the base from the back. **

In the diagnosis of his first-published species of the genus, Pleurothyrium poeppigii, Nees elaborates further his description of the staminal cycles. He notes 6 glands, alternating with the lobes at the height of the stamens, thick, fleshy, glabrous, yellow, contracted from the wide base into an obtuse acumen twice the width of the base, without (in the dried state) showing an indeterminate crease, within furnished with broad, obtuse keels, stretching from the base into the bottom of the flowers; 9 stamens, clustered, short, small compared with the flower, glabrous, the 6 exterior (ser I & II) opposite the lobes of the perianth, the filaments narrow, shorter than the anthers, the anthers subcubical, in the transverse diameter slightly larger, obtuse, the apex bent forward, a little more extrorse, the interior face a little more swollen; lateral locules in pairs, ovate, parallel, subequal, produced from the base almost to the apex, dehiscent by valves from the bottom to the top, the exterior locules of each pair slightly lower and turned about retrorsely, the interior, however, turned introrsely; the anthers of the third or inner cycle (ser III) of stamens conform to those of the rest, the filaments slightly shorter and broader than those of the latter, the glands at the base of these are obsolete or, rather, entirely confluent with the glandular base of the flower.

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*I have not studied fruiting material of this species; nor can I visualize the structure of the fruiting cup here described.

**Biglandular staminodia have not been noted in our material.

Actually, Nees described the floral structure as it appeared to him. The 6 glands alternating with the 6 lobes (the term "tepal" is used for these structures in Lauraceae) of the perianth do not arise from the mouth of the tube, but are attached in pairs to the outer staminal cycles (ser I & II) each gland in the form of an arc seeming to clasp the filament of the stamen from which it arises; on the introrse surface, these glands are often confluent, obscuring those glands which are associated with the other cycle of stamens; the third cycle usually bears smaller glands, more or less obscured by those of the outer cycles; or the glands may be so fused as to lose their identity and thus appear to be lacking altogether. Nees does not elucidate further here on the locules of the anthers.

Under his third species, P. bifidum, Nees states that the stamens form a slender, regular disk surrounded by a broad, 6-sinuate belt of contiguous glands, in the sinuses of which are the 6 outer stamens, the 3 interior stamens surrounding the pistil; the stamens are glabrous, the anthers cubical, the locules ovate, the lateral pairs almost contiguous at the apex, one locule introrse, the other conversely more retrorse. (I take this to mean that, seen laterally, the 2 locules appear one above the other, but in a different vertical plane, the upper introrse, the other extrorse.) Because Nees has not taken into consideration the origin of the tissues of the so-called "disk", his description does not give an accurate picture of the structure or origin of the staminal cycles.

Shortly after Nees' introduction of Pleurothyrium, Endlicher in his Genera Plantarum (1836-40, p. 320) published a diagnosis of the genus essentially the same as that of Nees, except for his interpretation of the staminodia as a fourth staminal cycle. Dietrich (1840, p. 1332) apparently copied Nees; Spach (1841, p. 472), merely assigns the genus to the Tribe Dicypellia.

Meissner (1864, p. 168; 1866, pp. 279-280) refers to an hypogynous disk adnate to the tube of the calyx, the free apex of the disk inflexed above the ovary, forming a narrow ring bearing stamens and glands. The 9 fertile stamens inserted in the orifice on the epigynous ring are free, subequal, and much shorter than the calyx; the 6 outer ones opposite the lobes of the calyx, alternate with the 6 sessile, ovate, flattened glands which are protuberances of the ring;* the anthers are cubical-oblong, truncate,

* This is inaccurate; the glands arise at the base of the filament.

the four locules oval, placed in a nearly horizontal series, the outer facing the sides, the intermediate being slightly higher, facing introrsely in the outer series of stamens, extrorsely in the inner series; staminodia 3, small, triangular, eglandular;** the ovary included entirely in tube, free, ovoid, the style equalling the stamens; the stigma depressed-subcapitate; fruit unknown, undoubtedly surrounded by a truncate cupule provided with a duplicate margin.***

In his treatment of the Lauraceae in Martius' Flora Brasiliensis, Meissner is still preoccupied with the structure of the hypogynous disk in the flower of Pleurothyrium, but at the same time distinguishes the stamens of the third cycle with their pairs sessile glands arising at the base of their filaments. (In some instances, one is able to separate the inner cycle easily from the outer and note the smaller size of the more or less discrete glands of the latter.) Meissner's lengthy description of the anthers does not give a clear image of their structure. He speaks of the four locules being in a nearly horizontal plane but does not mention the parallel vertical planes in this connection.

Baillon (1870, p. 438, 439; 478) is the first author to report the occurrence of a thick obconical receptacle, clothed (with pubescence) within a thick disk which more or less curves at the apex (presumably the glands first mentioned by Nees.) He describes 9 fertile stamens with the perigynous perianth inserted outside the margin of the disk; the 6 outer alternating with the lobes of these; the 3 inner (ser III) biglandular at the base; the filaments thickish, the anthers thick, cubical-oblong, their four locules placed in series at length almost horizontal; the exterior sublateral, the intermediate (locules) situated slightly higher facing, in the 6 outer series, introrsely, in the interior (ser III), extrorsely, the 3 sterile staminodia (ser IV), small or none; ovary free, included in the receptacle; the berry surrounded by the receptacle, developed in fruit, truncate at its apex. Baillon believes that Pleurothyrium differs from Nectandra in minor or secondary characters only.

**Meissner's is the first mention of the staminodia being eglandular.

***The suburceolate calyx surrounding the young fruit frequently bears the remains of the lobes and staminal cycles; this condition might give rise to the impression that the margin of the mature cupule would be double.

A consideration of the foregoing reveals the fact that the "disk" carried through literature for the past century and a half is made up of glands arising from the bases of the six stamens (ser I & II) of the two outer cycles which have become confluent through the pressure of growth. The sinuses of the disk, mentioned by Nees in his description of P. bifidum, are relics indicating the points of separation of the once discrete glands. In addition, there is the convex pubescent projection (the obconical tube mentioned by previous authors) on which seemingly the ovary, the three cycles of stamens with their associated glands and the staminodia, all of which cycles actually arise from the "epigynous" ring of Meissner which, if it is not a true hypanthium, is analogous to the latter structure.

Bentham and Hooker (1880, p. 159) accept Meissner's interpretation of the narrow ring formed by the hypogynous disk.

Mez (1889, p. 468) seemingly was the first student of the Lauraceae to understand the structure and origin of the "disk" mentioned by previous authors. In his key, he separates Ocotea and Nectandra from Pleurothyrium by the presence in the latter of 2 frequently confluent glands at the base of all stamens. He describes the 4-loculed anthers as subcapitate, the 2 upper loculles of the 2 outer series of stamens (ser I & II) introrse, the 2 lower, extrorse or rarely laterally dehiscent; the 2 upper locules of ser III, laterally dehiscent and the 2 lower introrse. To my knowledge, the fruit has not been noted since Nees spoke of a "berry" in the early stages of development.

Mez observed that the singular genus, closely associated to none, is easily and naturally separated by nature of the glands and anthers. He notes three species which seem to show affiliation with Pleurothyrium. Ocotea undulata and Nectandra trianae, both calling to mind the structure of the anthers of Pleurothyrium; but they appear distinct because of the lack of glands of the stamens of ser I & II; and Ocotea bahiensis which, provided with eighteen glands, shows an entirely different form of anthers.

Pax (1889, p. 116), on the other hand, still adheres to the theory of the fleshy disk surrounding the filaments at their base and spearated into six teeth alternating with the stamens.

Species were described by O. C. Schmidt (1928, p. 235) with "all stamens surrounded at base by two large, confluent glands, the anthers subrectangular...."

Macbride (1938, pp. 929-931) in his Flora of Peru gives only a basic generic description which differs from previous treatments in stating that the perianth tube is rarely well defined. Apparently he has not seen the fruit described by Nees. Since Nees' publication, Macbride seems to be the first to question the validity of the genus Pleurothyrium in relation to Ocotea.

Lasser (1942, pp. 118-19) published descriptions of two species from Venezuela in which he describes the anthers as subglobose. An illustration of Pleurothyrium reflexum shows a lateral (or profile) view of a stamen of the outer series--the first depicting the actual structure of the stamens of the genus.

The important contributions of Kostermans (1952, 1957) are discussed at the end of this paper.

Hutchinson (1964, p. 138) separates Pleurothyrium from the rest of the tribe Cinnamomi by: Flowers bisexual; staminodia of the 4 cycle present, thickened at the apex; disk well-developed, 6-lobed. His description goes back to Nees' diagnosis of P. bifidum.

Of the early students of the Lauraceae, only Nees and Meissner made any attempt to describe the differences that they observed that prompted them to recognize Pleurothyrium. I have gone into the history of their treatments at such great length because, inspite of the lack of clarity of their descriptions, and the lack of any supporting illustrations, both of these taxonomists recognized an entity distinct and separable from Nectandra and Ocotea. The latter genera are, for the most part, as I hope to demonstrate in a forth-coming paper, distinct from each other.

In his Historical Survey of the Lauraceae, Kostermans (1952, pp. 22(121), 23(122)) brought the history of Pleurothyrium up to date. Because he considered the character (the number of glands) used by Mez to delimit Pleurothyrium to be of no generic value, he has reduced the latter to Ocotea. Mez and Kostermans agree that the position of the anther locules, likewise, is of no generic value. But, both failed to take into account the strongest character brought out by Nees--the consistently distinctive shape of the anthers which separates the two genera.

Subsequently, Kostermans (1957, p. 39) has seen fit to combine all three genera, Ocotea, Nectandra and Pleurothyrium under Ocotea. If we accept this reduction, the entire taxonomic fabric

of the Lauraceae will be further imperiled; for elsewhere in the family there are several instances where reasons equally strong can be found for combining genera hitherto maintained as distinct entities by all students of the Lauraceae.

To summarize: I continue to maintain the three genera Ocotea, Nectandra and Pleurothyrium. The accompanying figures show the essential differences in the staminal cycles of the three taxa. The characters that I believe to be useful and valuable appear in the following key. Until the fruit of Pleurothyrium becomes well known, the key must, unfortunately, be based entirely on floral characters supported by secondary characters. Only when flowers and fruits of the known species are collected from the same tree can we be sure of obtaining the essential data.

KEY TO THE GENERA

NECTANDRA, OCOTEA AND PLEUROTHYRIUM

1. Stamens (with one known exception) of ser I & II without glands; anthers of ser I & II when viewed laterally more or less falcate, their four locules occurring on the introrse surface.

2. One pair of locules in the upper half of the anther, the other pair in the lower (introrse view) ..... OCOTEA

2. Four locules in ascending arc formation (introrse view; ser I & II); in descending (reverse) arc formation, upper pair lateral, lower pair extrorse (extrorse view; ser III ..... NECTANDRA

3. Anthers ovate, fleshy, papillose, attentuate; connective tissue abundant.... Section Pomatia

3. Anthers usually broader than long, transversely oblong or subreniform; connective tissue absent; locules occupying entire anthers .... Section Porostema

1. Stamens (with two known exceptions) of ser I, II & III with glands; anthers of ser I & II inclined, oblong, approximately isodiametric; the upper pair of locules directed inward, the lower pair, outward, but viewed laterally one of each pair visible ..... PLEUROTHYRIUM

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EXPLANATION OF PLATE

Fig. I. Pleurothyrium

Ze, stamens, ser I & II, ventral.
Ze', stamens, ser I & II, dorsal.
Ze", stamens, ser I & II, lateral.

Zf, stamens, ser III, ventral.
Zf', stamens, ser III, dorsal.
Zf", stamens, ser III, lateral.

Fig. II. Ocotea

Ae, stamens, ser I & II, ventral.
Af, stamens, ser III, ventral.
Af', stamens, ser III, dorsal.
Af", stamens, ser III, lateral.

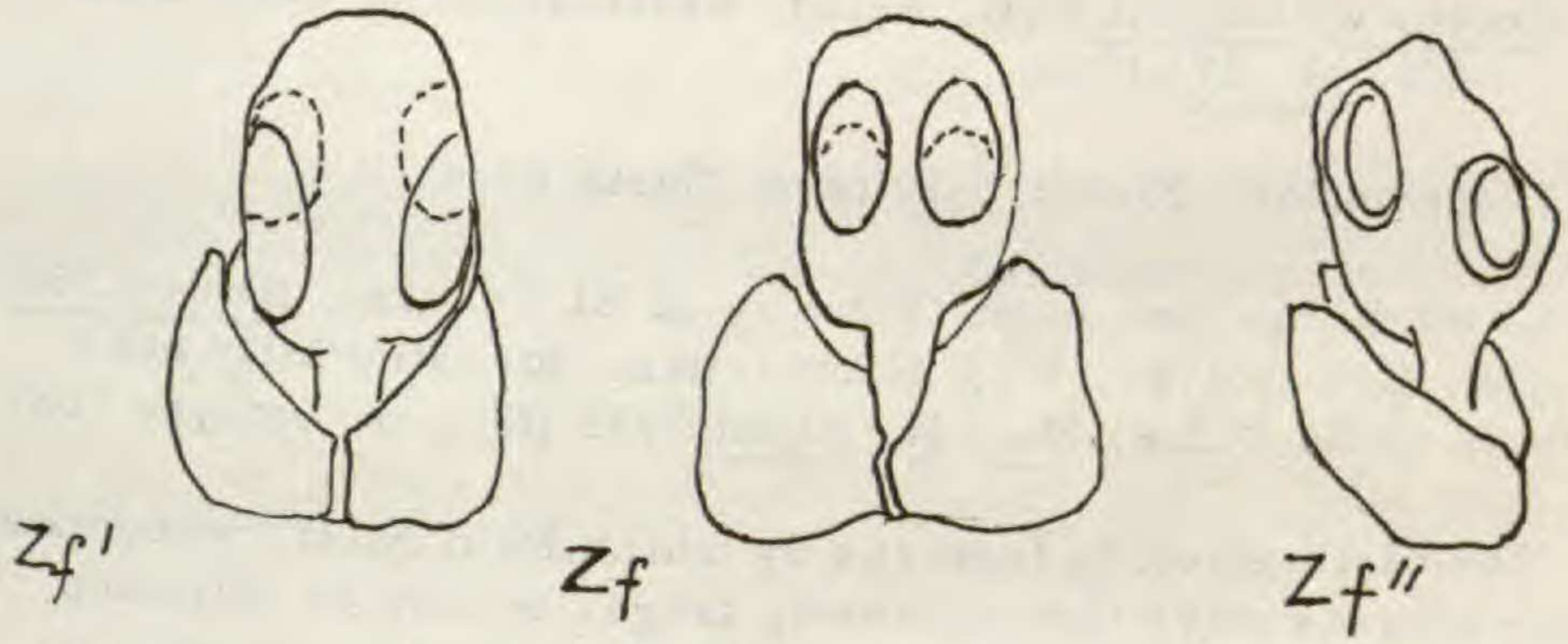
Fig. III. Nectandra Section Pomatia

Ze, stamens, ser I & II, ventral.
Zf', stamens, ser III, ventral.
Zf', stamens, ser III, dorsal.
Zf", stamens, ser III, lateral.
Zg, staminodium, ser IV, ventral.

Fig. IV. Nectandra Section Porostema

Ze, stamens, ser I & II, ventral.
Zf', stamens, ser III, ventral.
Zf', stamens, ser III, dorsal.
Zf", stamens, ser III, lateral.
Zg, staminodium, ser IV, ventral.

FIG I



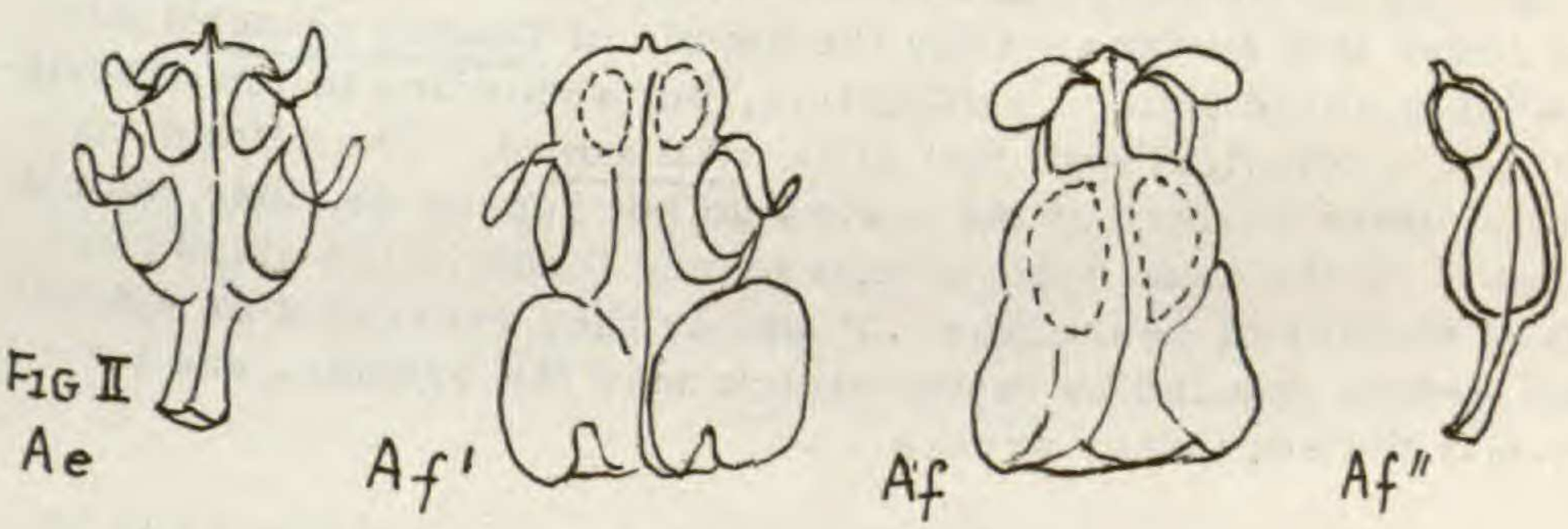


FIG II

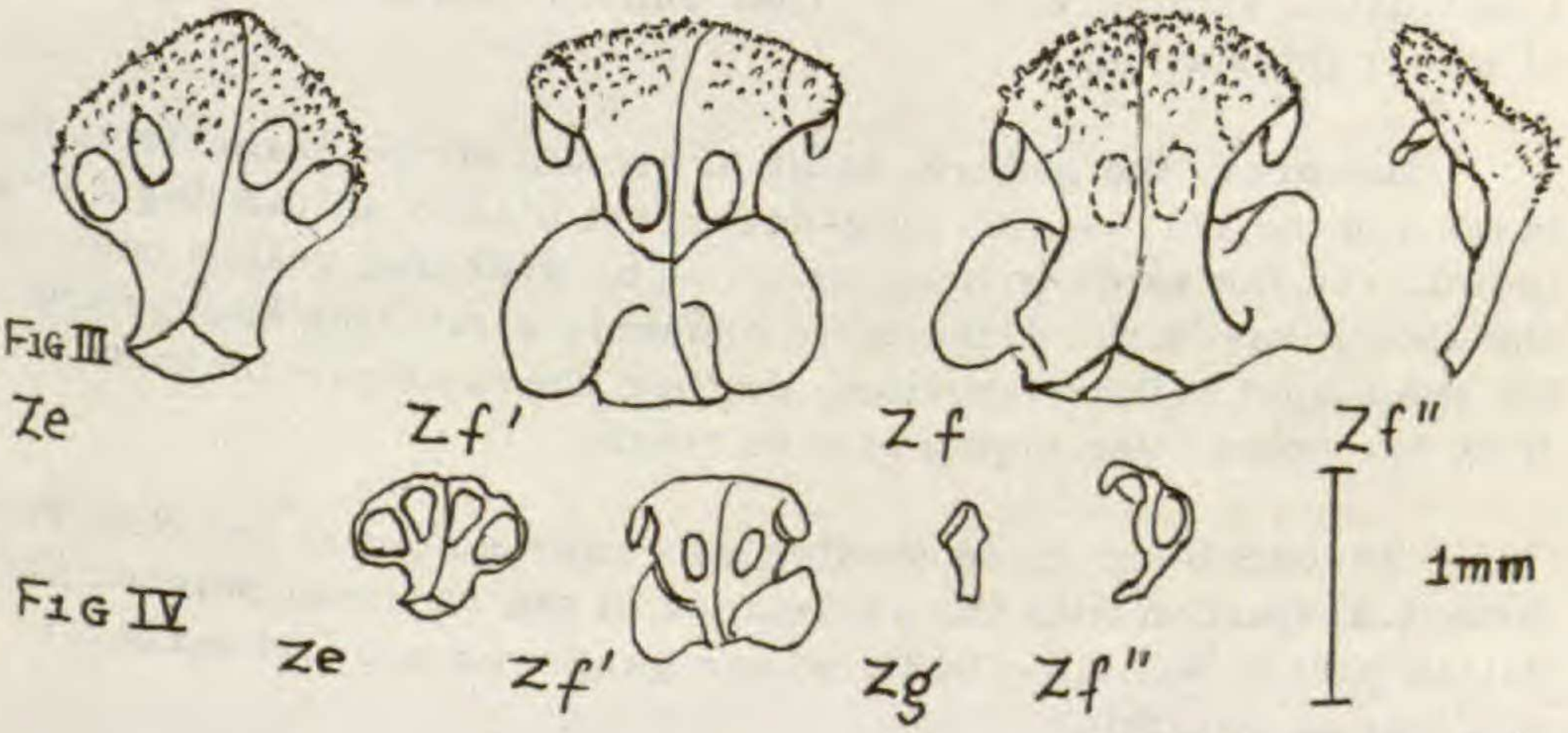


FIG III

FIG IV